Methodology in avian macrosystematics

by Walter J. Bock

Received 9 March 1992

Introduction

Interest in avian macrosystematics has a history that extends for over 200 years from the early beginnings of systematics. Analysis of this history is in itself a most interesting subject as the advances made over the past 200 years have been irregular and plagued with pitfalls, stops and starts, with periods of great activity interspersed with little to no work. An adequate historical review of avian macrosystematics does not exist, but cannot be undertaken here.

Macrosystematics includes 2 separate and quite different explanatory systems, with distinct modes of group hypotheses and disparate patterns of testing against secondary hypotheses and finally against empirical observations (Bock 1973: 391, 1977, 1981). These are: (a) explanations about the evolutionary relationships of organisms expressed in systems of biological classification; and (b) explanations about the pattern of phylogenetic branching expressed in a phylogenetic diagram. In both explanatory modes, groups of organisms are recognized, but the nature of these groups differ sharply from one another (see below). To be complete, the findings of any macrosystematic analysis should be expressed both in a biological classification and in a phylogenetic diagram, each of which provides different types of information about the organisms. Many systematists, e.g. cladists, argue that these 2 modes of explanation represent the same information; consequently, cladistic classifications are redundant with diagrams of phylogenetic branching. This approach is rejected by evolutionary systematists as lacking important information contained in evolutionary classifications. Both modes of explanation are equally important, but here I limit my discussion to the formulation and testing of biological classifications, with the clear realization that this is only one part of avian macrosystematics.

During the past 200 years, considerable advance has been achieved in recognizing many of the major groups of birds (orders and families), although considerably less understanding has been reached in clarifying the relationships of these groups to each other. Many, indeed most, of the groups we recognize today, such as waterfowl (Anatidae), pigeons (Columbidae), parrots (Psittaciformes), woodpeckers (Picidae), among many others, are accepted by all ornithologists. In this way, some natural groups of birds can be said to be robust, that is, recognized by all workers regardless of their approach to systematics, or which characters are used in the analysis, and how well or poorly the characters have been analyzed. Pigeons are pigeons, parrots are parrots, gulls are gulls, owls are owls. Even the novice in avian systematics will assign species correctly to these robust groups. The real test of our understanding of avian macrosystematics—especially our comprehension of the methodology used to formulate and especially to test, classifications—comes with the many unresolved general systematic problems in birds, such as: what are the relationships of the Hoatzin (*Opisthocomus*)?; are the Piciformes a natural group?; are the palaeognathous birds and the ratites monophyletic groups?; what are the relationships of the Pteroclidae?; or of the Coliidae?; or of the Trogonidae?; or of the Cathartidae?; or of many families of oscine birds within this suborder? It is naive to claim that even the best methodology will solve all taxonomic problems as some avian groups may prove stubbornly resistant to the best attempts to resolve their relationships.

The past 40 years have proven to be a period of exceptionally high activity in avian macrosystematics, following a half century of sluggishness. During these 40 years, greatest emphasis has been placed on the discovery of new taxonomic features to supplement traditional morphological features used for the previous 150 years. Initially, considerable emphasis was given to behavioural features, but this interest was short lived. Subsequently, more and more attention was given to chemical features, such as egg-white proteins (Sibley 1970, Sibley & Ahlquist 1972), blood proteins, lipids in secretions of the uropygial gland (Jacob, see Jacob & Ziswiler 1982), comparisons of total DNA content of the nucleus (Sibley & Ahlquist 1990), and finally sequencing of M-DNA (Shields & Helm-Bychowski 1988, Avise 1986) and of nuclear DNA.

Considerable attention has been given to whether a phenetic, a cladistic or an evolutionary approach provides the best biological classifications. Here, I restrict myself to consideration of a proper methodology for testing taxonomic hypotheses about groups, including the necessary analyses of taxonomic properties of characters. This methodology should be common to all approaches to classification, be they phenetic, cladistic or evolutionary.

During the past 40 years, considerable attention has been given to the analysis of large sets of taxonomic characters using sophisticated computer-based numerical techniques (generally some type of correlation analysis such as PAUP or Hennig86), in the attempt to obtain the best and most "parsimonious" classification. However, what has been almost completely lacking during the past 40 years are considerations of the analysis of the taxonomic characters themselves, both in theory and in actual studies. These methods include how different types of group hypotheses are tested against hypotheses about taxonomic properties of characters, how these character hypotheses are tested themselves against empirical observations, and the role of functional and adaptive analyses in character analysis. Theoretical papers such as Cracraft (1981a), Raikow (1985), Cracraft & Mindell (1989) and practical systematic studies, such as Cracraft (1974), Bledsoe (1988), Cracraft (1981b), Gauthier (1986), Swierczewski & Raikow (1981), Simpson & Cracraft (1981), Sibley & Ahlquist (1990), and McKitrick (1991), offer sweeping conclusions on the relationships and classification of birds, based, indeed, on intensive comparative description of old and new taxonomic characters and on elaborate computer-based analyses of data sets of these characters. But one will search in vain in these papers for any biological understanding of these taxonomic characters. In spite of the sophisticated methods used for describing some of the characters and of the excellent computer-based methodologies, these studies continue to be founded on character analyses predating Darwin's 'On the Origin of Species' and the subsequent acceptance of evolutionary concepts by biologists. Herein lies, in my opinion, the basic failure in avian macrosystematics.

One part of the solution lies in the clarification of the nature of biological classifications—what they are and for what purposes they are used—and the type of scientific explanation involved in establishing them. The other and perhaps the most significant part of the solution lies in the erecting of a methodology for the formulation of hypotheses at several levels and their testing, with careful attention given to the proper empirical observations used in the last step of the testing procedure. This methodology must be in close agreement with detailed aspects of accepted evolutionary theory, not just with a simplistic statement that organisms have evolved. If the evolution of phenotypic features results from selective demands arising from the external environment, i.e. is adaptive or coupled with adaptive evolution of other features, then the methods of macrosystematics must depend on functional-adaptive studies. The critical roles of these studies are in testing taxonomic properties of characters against empirical observations and in the establishment of degrees of confidence in the conclusions of these tests. These are topics on which I have devoted considerable effort and have published a series of papers (Bock 1959, 1965, 1967, 1969, 1973, 1977a, 1977b, 1978, 1979, 1980, 1981, 1988, 1989a, 1989b, 1990, 1991, Bock & de W. Miller 1959, Bock & von Wahlert 1965, Szalay & Bock 1991), to which the interested reader is referred for a full theoretical foundation of the points made in this paper.

It should be stressed that the ideas developed in these papers on hypotheses formation and testing and on the essential role of functional/adaptive studies are valid regardless of the approach to classification. Although these ideas are dependent on a full understanding of evolutionary theory, they are not restricted to evolutionary classification, but are equally valid for cladistic and phenetic approaches to classifications. However, a clear distinction must be made between a cladistic approach to classification and the so-called cladistic method of analysis; I consider the latter to be scientifically invalid (Bock 1981: 15). A distinction should also be made between cladistic and phylogenetic methods. Moreover, the various computer-based methods for formulating classifications on data sets, such as Hennig86 or PAUP, will work equally well with characters analyzed using these methods, because they depend only on an ordered character set and do not depend on how one has determined the information about the characters and their states.

These theoretical concepts will be illustrated by the use of several actual examples, in which more convincing conclusions have been reached using the methods mentioned above when compared with studies in which functional-adaptive investigations were not used.

THE CONCEPT OF BIOLOGICAL CLASSIFICATION

The concept and use of classifications in any science, including biological classification, are generally poorly understood in spite of their widespread use. Simply put, classifications are heuristic systems, no more and no less

(Warburton 1967, Bock 1973), but none the less valuable, and careful attention should therefore be given to their form and testing. As heuristic systems, classifications can be constructed according to any set of ideas or criteria depending on how the classification is used. For classifications to be 'natural' or 'general reference systems', they must be formulated according to the primary theory of the appropriate science. Evolutionary theory is the foundation for biological classifications, and hence they should reflect evolutionary theory as closely as possible. By evolutionary theory, I do not mean simply that living organisms have changed over time, rather I mean all aspects of this theory (e.g. "the five theories of evolution of Darwin"—Mayr 1982: 505, 1991: 36–7) including a detailed understanding of the causes and processes of evolutionary change. As emphasized by Hennig (1966: 8), it is complete nonsense to argue, as did Rosen *et al.* (1979), that a "natural order exists in nature", e.g., that "nature's hierarchy exists" independently of any theory and can be discovered with the use of a theory-free methodology.

As heuristic systems, classifications have a number of important uses (Warburton 1967, Bock 1973). Primarily, biological classifications provide the foundation for comparative studies in biology (see Bock 1989a for a discussion of the principles of comparison in biology). They summarize succinctly known empirical information about diverse organisms, and form the basis of information retrieval systems; but classifications are emphatically not information retrieval systems themselves and one cannot obtain directly from any classification the information used 'to construct', or better said to test, that classification. In addition, classifications serve as the foundation on which efficient and meaningful hypotheses can be generated about biological organisms for further research and testing, e.g. the prediction of unknown characteristics. The best natural classifications are those which permit the best summarization of known information and the best prediction of unknown features in diverse organisms.

It must be emphasized strongly that a classification and a phylogeny of a group, e.g. the class Aves, are not synonymous, but are 2 different and valuable methods to record conclusions reached in systematic analyses. Efforts by some systematists, e.g. cladists, to render these 2 systems of representation redundant to each other simply results in losing useful knowledge about the group; and as I have argued elsewhere (Bock 1977b, 1981), methods for testing classifications and for testing phylogenies differ distinctly from each other. Hence, a well carried out macrosystematic study should include in its conclusions both a clearly presented classification and a phylogenetic diagram.

Classifications and phylogenetic diagrams are related explanatory systems in biology and hence it is necessary to inquire into types of explanations involved in both classifications and phylogenetic diagrams. Many theoretical biologists and philosophers of science have claimed that evolutionary biology, being concerned with the history of organic life, is a strictly historical endeavour. A few philosophers have even claimed that because it is concerned only with the history of life, evolutionary theory is not part of science proper. Some systematists (mainly cladists) have claimed that all explanations in evolutionary biology, including systematics, are strictly nomological (Gaffney 1979, Platnick 1979, Platnick & Gaffney 1977) in a desperate effort to bring their work in line with Popperian concepts. Both positions are extreme and invalid, since evolutionary biology involves both nomological-deductive explanations (N-D E) and historical-narrative explanations (H-N E); I have outlined the distinctions between them in several papers (Bock 1981, 1988, 1991). Explanations associated with biological classifications (relationships between organisms) and with phylogenetic diagrams (branching of phylogenetic lineages) are clearly historical-narrative and as such are covered by the methods for formulation and testing H-N E, which depend on the N-D E within evolutionary biology including the known causes and processes of evolutionary change.

HYPOTHESES FORMULATION AND TESTING

If biological classification should reflect all aspects of evolutionary theory, so must the entire methodology of hypotheses formation and testing, including the predictions generated from various hypotheses and their eventual testing against empirical observations under the tenets of H-N E. First it is necessary to distinguish between group hypotheses and character hypotheses (Bock 1977b, 1981).

Group hypotheses in macrosystematics are of 2 types which differ sharply from one another both in their formulation and testing. The first are classificatory hypotheses about taxa which express the evolutionary relationships of the constituent members within a formal hierarchical system under the conventions accepted for evolutionary classification. This formal classification is a Linnaean hierarchy and the rules for recognizing the taxa are those that maximize simultaneously the postulated degree of evolutionary change and the sequence of phylogenetic branching of these groups. The taxa, once recognized, must be monophyletic in that the members of the taxon are descendants from a single ancestral taxon at the same or lower categorical rank.

The second type of group hypotheses are phylogenetic hypotheses about phyla (singular=phylon; see Bock 1977b: 877, 1981: 13) which express the pattern of phylogenetic branching within a formal phylogenetic diagram under the conventions accepted for these diagrams, namely successive dichotomous forks as advocated by Hennig (1966). Groups in this phylogenetic diagram are phyla which are closed descendent groups. The phyla, once recognized, must be holophyletic (Ashlock 1971), that is a group which includes the ancestral species and all descendent species. Phylogenetic hypotheses about groups can express ancestral-descendent relationships in addition to sister-group relationships. For an analysis of phylogenetic hypotheses about groups and their testing see Bock (1977b, 1981), as I restrict myself herein to classificatory hypotheses about groups.

Sequence of hypotheses formulation and testing

Although most taxonomic investigations are usually pursued with little to no attention given to the actual sequence of hypothesis formulation and testing, a definite order of these activities should be used in a formal analysis of macrosystematic methodology, and this sequence should be followed in written presentations (see Bock 1985a, 1985b, Bock & Morony 1978b, Bock & Bühler 1990, for examples). This sequence is as follows:

a) Formulation and statement of classificatory hypotheses about groups

These statements express hypotheses about the composition and evolutionary relationships of taxa which are monophyletic groups in the broad sense. Classificatory hypotheses should be explicit and stated at the beginning of a paper; they are within the realm of H-N E. Classificatory hypotheses are of the sort: is the genus *Diglossa* as recognized in Peters' Check-list monophyletic?; are the diverse species of flowerpiercers members of 2 distinct and not closely related genera, *Diglossa* and *Diglossopis*, within the Thraupinae (Bock 1985a)?; do the palaeognathous birds constitute a monophyletic group?; do the ratites constitute a monophyletic group (Bock & Bühler 1990)?; is the genus *Promerops* a member of the Meliphagidae (Bock 1985b)? Such hypotheses can be answered in the affirmative or negative.

Group hypotheses are easy to formulate, but this is not the important element in macrosystematics. The skill required is to be able to distinguish between those hypotheses worthy of further consideration for serious testing and those which can be disregarded for the present time. There are no reasons to consider seriously at this time, for instance, the testable hypothesis that the genus *Struthio* is a member of the family Corvidae. Moreover, one does not just formulate well-tested hypotheses, an expression used by some avian systematists. Rather, one should propose hypotheses worthy of consideration and then test them sufficiently so that they can be regarded as well-corroborated and usable as foundations for standard classifications and sequences. There are, of course, perfectly good classificatory hypotheses about groups which may not be worthy of consideration and testing at the current time because of an insufficient knowledge about the taxonomic features needed to test them. Formulating any classificatory hypotheses about particular groups and undertaking a comparative investigation of some feature do not of themselves provide a convincing basis for reaching sound conclusions about the classification of these taxa. Not all features are useful taxonomic characters.

b) Formulation and statement of character hypotheses about taxonomic properties of features

Secondary hypotheses about taxonomic properties of features are used to test the classificatory hypotheses about groups, and must be suited to the group hypotheses being considered—the secondary (=character) hypotheses must constitute valid tests regardless of the 'goodness' of the test. Valid tests of group hypotheses are those which relate predictions arising from the group hypotheses through the secondary character hypotheses to empirical observations according to the detailed stipulations of evolutionary theory. 'Good' tests are valid ones with a high ability to distinguish between correct and incorrect hypotheses—that is, possess a high resolving power to separate correct and incorrect answers. Taxonomic properties of features are those relative attributes of features, such as homology, plesiomorphy *versus* apomorphy, arising from the evolutionary history of the group. Hypotheses about taxonomic properties of features are H-N E. At some point within the test of such hypotheses must be appropriate N-D E, namely, the fundamental nomological aspects of evolutionary theory (see Bock 1981, 1988, 1991).

The only valid character hypothesis known to me for the testing of classificatory hypotheses about groups is homology (Bock 1977b, 1981, 1989b). Homologous features (or conditions of the features) in 2 or more organisms are those that stem phylogenetically from the same feature (or condition) in the immediate common ancestor of these organisms (Bock 1989b: 331). Hypotheses about homologues must always include a conditional phrase that describes the nature of the homology—i.e. the attributes of the feature in the immediate common ancestor. Conditional phrases are arranged into hierarchies – horizontal ones for the purposes of this analysis dealing with classificatory hypotheses.

Several widely used tests of classificatory hypotheses are, however, invalid (Bock 1981) and include those using criteria such as parsimony, or internal consistency or logic, or parallelism with changes in ontogeny, or distribution of character states in taxonomic groups. The last includes the almost universally used method of out-group comparison in cladistic analysis. This method is directly circular (Bock 1981: 15) because the test of the character hypotheses depends on the distribution of the character states in taxonomic groups and these character hypotheses are then used to test classificatory hypotheses about the same taxonomic groups.

The only valid test of hypotheses about homologues involves all forms of shared similarities between the presumed homologues; observations of these similarities comprise the objective empirical observations required in testing scientific hypotheses (Bock 1981, 1989b). Similarity of presumed homologous features is assumed to represent ‘ancestral similarity’, namely, the attributes present in the feature in the immediate common ancestor of the several organisms being compared, and which remained unchanged during evolution of the different lineages from the common ancestor. It must be emphasized that the defining criterion of homology is phylogeny and that phylogeny is defined in terms of evolution. Similarity is used to test hypotheses about homologous features, not to define the concept of homology. The difference between phylogeny and similarity is the distinction between the criterion used in *defining* theoretical concepts and that used in *testing* hypotheses about objects in nature presumably corresponding to the theoretical concepts. Only after being tested positively using empirical observations of similarity, are homologous features in diverse organisms then used to test classificatory hypotheses about taxa containing these organisms. No circular reasoning is involved in this analysis as frequently argued. Homologous features are not ascertained and tested by the phylogeny of groups and then used to test the phylogeny of these groups.

c) Establishing degrees of confidence

After testing and accepting hypotheses about the homology of features with properly stated conditional phrases, the next step is to estimate a degree of confidence (‘goodness’) for each homology, since the only valid test of hypotheses about homology distinguishes between correct and incorrect ones very poorly. If the hypothesis about the homology *has been accepted*, then the determination of a degree of confidence does not increase its acceptance. As is well known similarity of features in diverse organisms can be homoplastic as the result of independent origin and convergent evolution. Estimation of a degree of confidence in a particular homology is a probability measure, considering concepts of Bayesian probability, and depends largely on approximation of the probability that the features involved originated and underwent similar evolutionary change independently. These estimates must be based on the accepted principles of evolutionary change and on the evolutionary changes possible in the class of features containing the homologues, that is, how bones evolve, how muscles evolve, etc. Essentially, they depend on functional and adaptational analyses of the features, with the postulation of possible transformation sequences (that is, phylogenetic reconstruction series) based on these analyses.

Estimating the degree of confidence in accepted hypotheses about taxonomic properties of features is that aspect of systematics usually termed 'weighing of characters' or 'ascertaining the taxonomic value of characters'. Most discussions of character weighing, although inherently reasonable, have never been placed on a sound theoretical basis. Moreover, evaluation of degrees of confidence must be done *a priori*, not *a posteriori*, to the use of these character hypotheses in testing group hypotheses.

The degree of confidence will depend strongly on the complexity of the actual feature, its relationship with factors of the external environments and hence with selective demands, and whether the feature is appearing or being lost in evolution, etc. If the homologous feature is a simple one, such as the brown colour of the plumage in different species of sparrows which serves as protective colouration, then one may well assign it a very low degree of confidence. If the feature is a complex one, such as the Weberian sound-transmitting ossicles derived from vertebral processes in a number of fresh-water teleost fishes, one is justified in estimating a high degree of confidence. Generally, the degree of confidence is higher in homologues which have appeared and are becoming more complex during their evolution than in those which are disappearing or becoming simpler. Many of the considerations given by taxonomists about criteria for homology (e.g. Rieger & Tyler 1979) or to an estimate of the taxonomic values of different characters (Hecht & Edwards 1977) are actually methods establishing confidence in accepted conclusions about homologies.

Estimation of these degrees of confidence is an absolute requirement in macrosystematic analysis because so many apparent homologues have an exceedingly low probability of being correct. It is simply not valid to use equally all successfully tested homologies in the testing of group hypotheses. Homologies with low degrees of confidence have little or no value in tests of group hypotheses, contrary to the beliefs of many systematists. Unfortunately no studies have been done using the concepts of decision theory on the contribution of homologues with varying degrees of confidence in accepted group hypotheses. However, some rough estimates suggest that even several hundred independent homologues, each having a degree of confidence of less than 10% will provide a poor test of a group hypothesis. A much smaller number of independent homologues, perhaps 10 or even fewer, each having a degree of confidence of over 90% may provide a very convincing positive test of a group hypothesis. The long lists of untested postulated homologues given in numerous taxonomic papers may appear convincing at first glance, but they become far less impressive when one realizes that no attempt has been made to state the hypotheses of homologies clearly, let alone to establish degrees of confidence in the homologues involved. Generally little work is required to demonstrate that most of the homologous features in the long lists possess low levels of confidence.

d) Testing of group hypotheses

Each classificatory hypothesis about groups is tested against a number of separate character hypotheses about homology, each of which has been tested against empirical observations completely independently of the others. As already indicated, increase in the degree of confidence in group hypotheses is gained with increase in the number of tests against different homologous features possessing a high degree of confidence.

Each empirical test of a character hypothesis about homologies must be absolutely independent of all others. Otherwise the different homologues will not provide independent tests—they are redundant—as stressed by Bock (1977, 1981, 1989b). Examination of the criteria for homology advocated by some authors (e.g. Remane 1952), demonstrates that some are either not independent of other homologues or are not independent of the group hypothesis being tested. Homologues tested with such criteria would not provide additional independent valid tests of the group hypothesis and hence would not increase the confidence in the correctness of the group hypothesis. Continued testing of a group hypothesis against more and more character hypotheses possessing low degrees of confidence simply does not add to the confidence already attained.

The single major defect in many papers on macrosystematics lies in the use of character hypotheses possessing low degrees of confidence for testing group hypotheses. Close examination of the large number of taxonomic characters cited by Gauthier (1986) supporting his conclusion that birds are most closely related to the Coelurosauria of the theropod dinosaurs finds only low degrees of confidence in the homologues; therefore his group hypothesis has a corresponding low degree of confidence. McKitrick (1991) has recently published a most interesting phylogenetic analysis of birds using their hindlimb musculature; she presents a phylogeny and compares her conclusions with various recent classifications, but she does not present any classificatory hypotheses herself. Close study of McKitrick's paper suggests that a serious shortcoming lies in the low degree of confidence in the homologies of the several character states described for each hindlimb muscle; hence any classificatory hypothesis about avian taxa tested against these homologues would have a correspondingly low degree of confidence.

The recently published classification of birds by Sibley & Ahlquist (1990), advocating major modifications in the relationships of avian orders and families, depends entirely on the degree of confidence that can be established for the homology of avian DNA, in as far as Sibley & Ahlquist have described and compared it in the diverse taxa of birds. It must be emphasized that they have never described the homologies of the fragments of DNA subjected to the annealing comparisons used in their analysis and have therefore presumably never tested the homology of these DNA fragments directly; nor have they provided any estimate of the degree of confidence for each conclusion about the fragments of DNA. They have merely presumed them to be homologous and have assumed a high degree of confidence in *all* homologies regardless of the extent of annealing of DNA from different taxa, even at the lowest percent of annealing. Contrary to the claims of Sibley & Ahlquist and some other workers, they have not solved the 'problem of homology'. If one concludes, as I do, that the degree of confidence is low for each (unstated) individual test of homology of the many different fragments of DNA in the comparisons made by Sibley & Ahlquist, then the degree of confidence in their classificatory hypotheses would be correspondingly low. The fact that the annealing comparisons involve a large number of fragments of the DNA of the taxa compared does not raise the degree of confidence, as they claim, in the test of the group hypotheses. The degree of confidence in a group hypothesis is *not* ascertained by a simple addition of the degrees of confidence of the individual character hypotheses used to test the group hypothesis. Rather the degree of confidence in the group hypothesis is largely determined by the degree of confidence in the individual character hypotheses.

e) The method of reciprocal illumination

A major point made by Hennig (1966: 21) is that "In reality, phylogenetic systematics uses a method known and employed in all sciences, which in the humanities is called the 'method of reciprocal illumination' (checking, correcting and rechecking of the Anglo-Saxon authors)." Hennig suggests that this method involves the formulation of a series of character hypotheses, and from this series a group hypothesis is generated, which in turn is then used to check further the validity of the original character hypotheses which in turn are again used to check further the group hypothesis (Hennig 1966: 22). If I understand this statement correctly, it is circular in spite of the strenuous protesting of Hennig against this conclusion. This method has been cited with approval by cladistic systematists and a number of philosophers of biology, but without real clarification of the exact procedure employed. Either the method of reciprocal illumination as outlined by Hennig is circular or the description of the proper working procedure is obscure. "Checking, correcting and rechecking" can be interpreted completely differently, as an approach which involves the testing of a group hypothesis using a series of independently tested character hypothesis, thereafter reformulating the group hypothesis depending on the outcome of these independent tests, followed by further testing of the modified group hypothesis using a series of independently tested character hypotheses, including new ones not used in the test of the original group hypothesis. Bühler (1980) outlined this approach within the realm of

N-D E in functional morphology. This is a completely different approach from that described by Hennig as I understand it. If this is the approach to be used, then the better name would be 'the method of multiple independent tests' rather than 'the method of reciprocal illumination'.

CASE STUDIES

If the above argument on the central role of functional-adaptive analyses in macrosystematics is acceptable, then it should be possible to demonstrate with case studies that the use of this approach has permitted a better understanding of difficult problems in macrosystematics.

Relationship within the plovers (Charadriidae)

In a series of papers, P. R. Lowe (see 1922; see also Bock 1958 for citations to other papers) discussed the relationship of charadriid genera based largely on the ossification of the supraorbital rims of the brain case and the colour of the back. He argued that the primitive genera possessed less ossified supraorbital rims and a light dorsal colour and that the advanced genera had more ossified supraorbital rims and a dark dorsal colouration. Although reviews critical of Lowe's papers were published, many of his general conclusions formed the basis of the classification of this family in Peters' Check-list. Nowhere in his papers did Lowe attempt any functional-adaptive analyses; he judged that the less ossified supraorbital rims and lighter colour were primitive ("adumbrated"), claiming these were the initial attempt by nature to produce these features, and that the more ossified rims and darker colour are the more complete (finished) product. In addition, he claimed that the primitive, less ossified supraorbital rims represented the earlier stage in the ontogenetic development of these rims, through which the more ossified rims passed earlier in their ontogeny. He argued strongly that these features are not directly affected by the present-day environment, but represent conditions inherited unchanged from the ancestral state.

In analysing these features in my generic review of the plovers (Bock 1958), I found the colouration of the dorsum easy to explain. Ever since Professor Alfred Newton suggested to H. B. Tristram in 1858 (letter dated 24 August 1858—Wollaston 1921: 111–117) that Tristram should read the then recently published papers by Darwin and Wallace to explain the observed diversity of dorsal colour in African larks, there have been numerous papers showing that the dorsal colouration in open country birds such as plovers, larks, etc. matches the colour of the substrate closely as protective colouration. For Lowe to claim otherwise would require extensive supporting evidence which he did not provide. Alteration in dorsal colour would occur rapidly in the evolution of different species of plovers accompanying changes in the colour of the substrate. Moreover, this evolutionary change would readily occur independently and would revert equally readily with reverse modification of the substrate colour.

The degree of ossification of the supraorbital rims is almost equally easy to explain in terms of functional and adaptive significances. Ossification of these rims is inversely correlated with the size of the nasal glands lying in a supraorbital position; larger glands press more on the bone, cause its de-ossification and hence reduction in the size of the rims. These glands secrete salt and their size is directly correlated with the salinity of the environment of diverse species. Evolutionary changes in size of the supraorbital rims would track changes in the salinity of the environment, would occur independently in diverse species and would reverse with increase and decrease in environmental salinity. Indeed great changes in the size of the supraorbital rims can be observed in a single individual during its life correlated with changes in the salinity of its environment.

Hence it can be shown by rather simple functional-adaptive analyses that the different observed states in these 2 characters are either not homologous or, if concluded to be homologous in diverse species of plovers, they possess a very low degree of confidence, with no possibility of establishing which are the primitive and which are the advanced characteristics in present-day plovers. Their observed states possess a high degree of homoplasy because of their high probability of independent evolutionary origin and reverse evolution. Classificatory hypotheses about taxa within the plovers accepted after testing against Lowe's characters would have exceedingly low degrees of confidence because of the corresponding low degrees of confidence in the character hypotheses. In simple words, dorsal colouration and supraorbital rims in the plovers are poor taxonomic characters.

The palaeognathous birds

The palaeognathous birds comprise the larger flightless ratites and the smaller flying tinamous. The question of whether the palaeognathous birds or the ratites or both constitute monophyletic taxa has been argued by ornithologists ever since these birds were known. Originally the flightless ratites were considered to be a monophyletic group, but not closely related to the flying tinamous. T. H. Huxley (1867) placed the large flightless ratites in the Ratitae, and the tinamous in the Carinatae, together with the other carinate birds. Subsequently some workers (e.g. Wetmore 1940) placed the tinamous together with the ratites in a separate superorder, the Palaeognathae, a monophyletic group within the Neornithes. Gradually during this century most ornithologists have come to agree that the palaeognathous birds and the ratites are polyphyletic groups. Most avian classifications published after 1940 did not recognize the superorder Palaeognathae largely as a result of McDowell's conclusions (1948) that the palaeognathous palate is not homologous in these birds, but also because of the disjunct distribution of the flightless birds. The several families of ratites and tinamous were separated into a number of distinct orders which were placed next to one another in standard sequences simply because ornithologists had no clues to their relationships to other birds. However, a few workers (e.g. Glutz von Blotzheim 1958) still argued for the monophyly of the ratites leaving the question of the classification of the palaeognathous birds unresolved.

A resolution of this question was achieved a few years later when Bock (1963) showed that a complex suite of cranial characters are all homologous in the palaeognathous birds, namely the palaeognathous palate, the posterior position of the basipterygoid process and articulation with the pterygoid, the large zygomatic process lying along the lateral side of the quadrate and closely applied to it, the gap between the maxilla and the maxillary process of the nasal, and the continuity of the ossified orbital and nasal septa (resulting in rhynchokinesis). Moreover, the degree of confidence in these homologues was estimated to be high. All these features had been known previously, but a functional-adaptive investigation permitted the estimation of a high degree of confidence in the character hypotheses and hence in the classificatory hypothesis that the ratites and tinamous constituted a monophyletic taxon. No other classificatory hypotheses were proposed and tested. This classificatory hypothesis was supported by other workers, including Meise (1963), though he considered only the ratites.

The question of the interrelationships of the palaeognathous birds remained, with considerable diversity of opinions on the placement of some taxa within the entire group (Sibley & Ahlquist 1972, 1981, 1990, Cracraft 1974, 1981b, 1988, Bledsoe 1988). However, some conclusions were widely accepted. The tinamous were considered to be a separate taxon and a sister group of the monophyletic ratites. The ostriches and rheas were regarded as sister groups, forming a monophyletic taxon within the ratites.

In a subsequent study, Bock & Bühler (1990) tested a series of classificatory hypotheses, including: whether the Ratitae are a monophyletic taxon? (no); whether the Struthionidae and the Rheidae are sister groups? (no); whether the Struthionidae and perhaps the Aepyronithidae are a monophyletic taxon within the palaeognathous birds? (yes); and, whether the Tinamidae, Rheidae, Casuariidae, Dromaiidae, Apterygidae and Dinornithidae constitute a monophyletic taxon within the palaeognathous birds? (yes). These hypotheses were tested against character hypotheses about the homology of the complex tongue apparatus in these birds. A number of skeletomuscular attributes of the tongue apparatus present in the ostriches are not homologous with those present in the other palaeognathous birds. Moreover, it could be argued that the 2 different configurations of the tongue apparatus present in the palaeognathous birds could not have evolved from each other, but rather each type of reduced tongue evolved independently from a well-developed tongue in the immediate common ancestor of the 2 monophyletic taxa within the palaeognathous birds. The character hypotheses possess high degrees of confidence, and hence the group hypotheses tested against them also possess high degrees of confidence.

Bock & Bühler's classificatory hypotheses differed in several important aspects from previous conclusions. They concluded that the Ratites are not monophyletic within a monophyletic Palaeognathae, and that the Tinamidae is not the sister group of all ratites, but of the Rheidae. These conclusions are radically different from those presented by Sibley & Ahlquist (1981, 1990) based on DNA studies. Assessment of which of these disparate conclusions, if either, are correct depends largely on an evaluation of the degrees of confidence in exact character homologues, particularly of those DNA fragments used by Sibley & Ahlquist to test their several conclusions about palaeognathous birds.

Neotropical flowerpiercers

A small group of 10–17 species of Neotropical nectar-feeding birds found in the mountainous forests from Mexico to Argentina, commonly called flowerpiercers because of their method of cutting into the corolla of flowers to obtain nectar, had been placed in a monotypic genus *Diglossa* ever since their discovery until Bock's (1985a) classificatory hypotheses that the flowerpiercers are members of 2 genera, *Diglossa* and *Diglossopis*, and that these genera are not closely related to one another within the New World 9 primaried oscines, e.g., the Thraupinae. The hypotheses were tested against a series of character hypotheses about the homology of features in the skull, the corneous tongue and the rhamphotheca of these species. The conclusions that these features are not homologous in the 2 groups of species permitted acceptance of the classificatory hypotheses. A brief functional-adaptive analysis of the corneous tongue, which serves to obtain nectar, was critical to this decision and the accompanying conclusion that the 2 genera evolved flower-piercing habits and associated specializations independently.

The passerine finches

The classification of Old World finches has been a major problem for systematists from the beginnings of avian classification. During this century the passerine finches (*Passer* and its relatives) have usually been placed in the Ploceidae, sometimes in a separate subfamily as in Peters' Check-list. The discovery (Bock & Morony 1978a) of a unique neomorphic bone, the preglossale, in the tongue of these birds permitted the testing of the classificatory hypotheses that the genera *Passer, Montifringilla* and *Petronia* constitute a monophyletic assemblage and that this group is not part of the Ploceidae (Bock & Morony 1978b). These group hypotheses were supported by the homology of the preglossale, the presence (homology) of the M. hypoglossus anterior, and the homology of the 'seed-cup' in these genera. Functional analyses of the thick corneous tongue in seed-eating passerine birds as a seed-cup used to manipulate seeds during their shelling and an understanding of the evolution of muscles and bones in vertebrates gave the character and corresponding group hypotheses high degrees of confidence. This was contrary to the conclusions of Sibley & Ahlquist (1985: 144), which, however, they later (1990: 675–683) changed to agree with Bock & Morony without comment on their earlier conclusions. Although the affinities of the passerine finches to other oscine birds is still unresolved, their membership in the Ploceidae and the Estrildidae can be ruled out.

The South African sugar bird

The curious genus *Promerops*, or Sugar Bird, from South Africa has defied avian systematists in their attempts to place it within the system of oscine birds. It has usually been placed in a monotypic family or in the Australasian family Meliphagidae; the latter placement is puzzling because of the great ocean gap between South Africa and the range of the rest of the Meliphagidae. Sibley & Ahlquist (1985: 144, 1990: 670–675) concluded on the basis of DNA annealing that *Promerops* is a member of the Nectariniidae. Bock (1985b) tested the dual hypotheses that *Promerops* is a member of the Nectariniidae and that *Promerops* is a member of the Meliphagidae against character hypotheses on homologies of the skull and tongue apparatus. These tests do not support the hypothesis that *Promerops* is a member of the Nectariniidae. Especially important is the non-homology of the thick-walled, quadrifid, fringed, tubular tongue in *Promerops* and the thin-walled double-tubed corneous tongue with few broad, flag-like laciniae in the nectariniids. If *Promerops* is a nectariniid, then the common ancestor of *Promerops* and other nectariniids was not specialized to feed on nectar. Homologies in skull structure and corneous tongue of *Promerops* and of the meliphagids support the hypothesis that *Promerops* is a member of the Meliphagidae, but they do not possess high degrees of confidence. Although it is not possible at present to distinguish *Promerops* from the Meliphagidae, it is still possible that the South African Sugar Bird evolved from some other oscine family; but strong arguments can be raised against placement of *Promerops* in the Nectariniidae. It should be noted that Sibley & Ahlquist's argument that *Promerops* is closely related to the New Guinean genera *Toxorhamphus* and *Oedistoma*, and that these 2 latter genera are nectariniids must be examined carefully because these 2 genera share many homologous features of the tongue apparatus with those of the meliphagids and few, if any, with those of the nectariniids.

The piciformes

The monophyly of the Piciformes has been the subject of considerable dispute for the past decade, involving the question whether the families Galbulidae and Bucconidae (jacamars and puffbirds), which are often placed in a distinct suborder—the Galbulae, are members of the Piciformes. All major classifications of birds include the Galbulae in the Piciformes in spite of the thorough analysis of G. Steinbacher (1935), who showed that details of the distal tarsometatarsal condyles and other features associated with the reversed fourth toe in the zygodactyl foot of the Galbulae are strikingly different from those present in the Pici. Unfortunately, he never discussed the significance of his findings for the macrosystematics of the piciform birds. Although Steinbacher (1935: 277) spoke of 4 different '*bauplans*' of zygodactyl feet in birds, this expression is uninformative about their evolution. J. Steinbacher (1937) undertook further investigations of the Galbulae and concluded that they were properly placed in the Piciformes; he did not discuss the findings of G. Steinbacher. It is interesting that Stresemann (1959), who recognized many of Wetmore's suborders as distinct orders, retained the Galbulae in the Piciformes. In companion papers, Swierczewski & Raikow (1981) and Simpson & Cracraft (1981) analyzed the classification of the Piciformes and concluded that this order was monophyletic. Olson (1983) disagreed and concluded that it was polyphyletic and that the Galbulidae and Bucconidae are related to the Coracii (Coraciidae and their allies). Raikow & Cracraft (1983) countered Olson's conclusion. I would like to concentrate on the first part of Olson's conclusion, namely the polyphyletic nature of the Piciformes.

Olson is quite correct in calling attention to the different configurations of the zygodactyl foot in the Galbulae and Pici. Character hypotheses can be formulated as to whether the structural details of the distal tarsometatarsal condyles and associated ligaments of the zygodactyl foot of the Galbulae are homologous with those of the Pici as attributes of a zygodactyl foot. Testing these hypotheses against empirical observations of foot structure in these 2 forms of birds, results in rejection of the hypotheses. [It should be noted that contrary to the implication given by Olson (1983: 127), the earlier analysis of Bock & Miller (1959) was not concerned with the question of whether or not the several different types of zygodactyl feet as seen in cuckoos, parrots, galbulids and picids evolved independently; hence the earlier findings of G. Steinbacher were irrelevant to their analysis.] The functional-adaptive analysis presented by G. Steinbacher (1935) and later discussions of Bock & Miller (1959) can be used to argue that the non-homology of the zygodactyl foot in galbulids and picids has a high degree of confidence. The counter arguments presented by Raikow & Cracraft (1983) simply do not touch on the major points raised by Olson. Moreover, Raikow & Cracraft (1983: 134) commit a major error in stating that "We suggest that the zygodactyl conditions of the Galbulae and Pici are homologous because other characters (see below) corroborate the unity of the Piciformes." Testing and acceptance of a hypothesis on the homology of one feature cannot be based on a presumed affinity of the organisms possessing this feature or on a correlation with other presumed homologous features. By making this statement, Raikow & Cracraft remove the zygodactyl foot from any further use in testing group hypotheses about the Piciformes—a procedure which should be avoided in macrosystematics.

The South American hoatzin

Perhaps of all problems facing avian macrosystematics, the affinities of the hoatzin, *Opisthocomus*, is the most vexing. It was originally described in the genus *Phasianus* in 1776 and only placed in the monotypic genus *Opisthocomus* in 1811. Over the years this bird has generally been placed in the Galliformes or the Cuculiformes, or in a group (a separate order) intermediate between the two, but for the past century most workers have included the hoatzin in the Galliformes as a separate suborder. More recently Sibley & Ahlquist (1973, 1990) have concluded that *Opisthocomus* is a member of the Cuculiformes and is most closely allied to genera such as *Guira* and *Crotophaga*, originally on the basis of a comparison of egg-white proteins and later of DNA annealing. In their extensive discussion of the history of systematic analyses and characteristics of *Opisthocomus*, Sibley & Ahlquist fail to mention an important attribute of this bird (Bock, in press)—namely that the arrangement of the toes in the hoatzin is anisodactyl, not zygodactyl as in all members of the Cuculiformes. Examination of skeletons of *Opisthocomus* shows that this bird lacks completely the specializations described by G. Steinbacher (1935) for the cuckoo tarsometatarsus which are associated with their zygodactyl foot, permitting reversal of tendons to the fourth toe. The zygodactyl foot of cuckoos is an adaptation for perching and is so used in most forms of cuckoos, including those genera concluded by Sibley & Ahlquist to be the closest relatives of the hoatzin. Hoatzins are specialized for life in trees, and if they descended from cuckoos, there is no way that the hoatzin anisodactyl toe arrangement would have evolved from the cuckoo zygodactyl arrangement under selective demands for these habits (Bock & Miller 1959). Hence there is no way to support the conclusion that the hoatzin evolved from an ancestor with a zygodactyl foot such as possessed by cuckoos. Sibley & Ahlquist did not conclude that *Opisthocomus* was a sister group of the cuckoos, but that it evolved from an ancestor in the middle of the cuckoo radiation and therefore from an ancestor possessing a zygodactyl foot. Therefore testing the classificatory hypothesis that *Opisthocomus* is a member of the Cuculiformes against character hypotheses about the homology of toe arrangement would result in its rejection with a high degree of confidence because the arrangements of the toes in the Cuculiformes and in *Opisthocomus* are not homologous with any degree of confidence. At the present time, the position of *Opisthocomus* in the system of birds is uncertain, but it is not a cuckoo. Possibly it is a remnant of an old South American radiation most of which has become extinct; if so, the relationships of the hoatzin to other birds could be difficult to ascertain.

CONCLUSION

The theoretical discussion and the several case studies presented above demonstrate that a convincing classification of birds is almost completely dependent on thorough and proper analyses of character hypotheses, including the demonstration of high degrees of confidence in the taxonomic properties of characters used to test classificatory hypotheses about groups. Functional-adaptive investigations are the critical part of character analysis, both in the empirical testing of the character hypotheses and in the determination of their degrees of confidence. Therefore until avian systematists give careful attention to functional-adaptive investigations in the analysis of the taxonomic properties of characters, no convincing progress will be made in avian macrosystematics regardless of the efforts made in the search for new taxonomic features or in the development of computer methods for analyzing large numbers of characters to formulate the most 'parsimonious' classifications. After nearly 150 years since publication of '*On the Origin of Species*', the time has come to insist that macrosystematic methodology be formulated on evolutionary theory.

Acknowledgements

I would like to thank Dr. J. F. Monk for inviting me to contribute a paper to the Bulletin of the B.O.C. Centenary Supplement and for his excellent assistance in editing the paper, which is much improved through his efforts.

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Address: Dr Walter J. Bock, Department of Biological Sciences, Columbia University, New York, NY 10027, U.S.A.